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# Debunking paradigms in estuarine fish species richness

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ABSTRACT: The comparison of species complements within and between habitats and geographical areas is a fundamental aspect of ecological assessments. However, many influences resulting from variability in sampling and data analysis often hinder the ability to determine important patterns in community structure. The study is based on the hypothesis that, using a standard sampling method, an asymptote in the rarefaction curve represents the total (gear-specific) species complement likely to be encountered for the geographical area. Accordingly, an asymptotic species richness estimator was used to predict the full complement of species present within each estuary that could be caught using seine netting. The rarefaction curves and species richness estimator enabled the interrogation of 2 underlying paradigms of ecological species richness: the species–latitude relationship and the species–area relationship. This analysis revealed distinct groups which showed a significant relationship with latitude and size, although the size effect had a smaller influence. In particular, the species–latitude relationship paradigm held true in this study while the species–area relationship paradigm only applied when latitude was considered concomitantly. Marine species in particular appeared to account for the increased fish species number at lower latitudes. The underlying influence of latitude and estuary size suggests that any managerial tool that explores anthropogenic impacts (such as those used in the European Water Framework Directive) should include these aspects. This analysis gives environmental managers an objective cost-beneficial method of identifying when and where further sampling does not give further information for management.

KEY WORDS: Seine netting · Rarefaction curves · Fish species richness · Species–latitude relationship · Species–area relationship



## 1. INTRODUCTION

The importance of estuaries for freshwater, migratory, estuarine and many marine fish species is well described (Elliott et al. 2007a, Nicolas et al. 2010b), with their highly variable environments providing essential breeding, feeding and nursery habitats (Potts & Swaby 1993, Elliott et al. 2002, Elliott & Whitfield 2011, Potter et al. 2015). Estuaries and their catchments also support large urban and industrial areas, containing anthropogenic activities and pressures associated with development (McLusky & Elliott 2004, Cardoso et al. 2011, Vasconcelos et al. 2015).

Continued and recent requirements for effective management have led to the exploration of the relationships between biogeography, geomorphology and fish diversity in estuaries at global, regional and local scales (França & Cabral 2015, Pasquaud et al. 2015, Vasconcelos et al. 2015). Exploration of the complex nature of factors, including the controlling hydrophysical elements that can affect fishes in estuaries, suggest 2 underlying fundamental paradigms that aim to explain the fish species richness in estuaries. Firstly, species richness appears to increase with waterbody size (Gleason 1922, Nicolas et al. 2010b) in which the species–area relationship (SAR) as-

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sumes that larger waterbodies support a higher number of species as they likely provide a greater diversity of habitats and therefore a higher availability of ecological niches (Pease 1999, Pérez-Ruzafa et al. 2007, Franco et al. 2008a). Secondly, species richness appears to decrease with increasing latitude (Gaston 2000, 2007, Vasconcelos et al. 2015). This relationship, henceforth identified as the species–latitude relationship (SLR), has been confirmed for estuarine fish assemblages investigated at the global scale (Pasquaud et al. 2015, Vasconcelos et al. 2015). Although not so for fishes, its validity at a smaller geographical scale (spanning less than 3° in latitude) has been shown for other groups (Gotelli & Ellison 2002). The SLR relates generally to the balance between the speciation/immigration and extinction/emigration of species resulting from the combination of multiple mechanisms, including geographic area, productivity, ambient energy and evolutionary speed, among others (Willig et al. 2003).

Species richness is a metric commonly used to assess the status of estuarine fish assemblages across the Northeast Atlantic (Pérez-Dominguez et al. 2012, Lepage et al. 2016), under the requirements of the European Union Water Framework Directive (2000/60/EC; WFD 2000) that a 'good ecological and chemical status' is achieved in all European waterbodies. Where this condition is not met, management measures are to be implemented, and therefore it is of paramount importance that the assessment is based on a good understanding of the structure and functioning of the system under management and that appropriate and sound indicators are used (Hering et al. 2010). These indicators (e.g. fish species richness) need to be independent from confounding factors such as, for example, variable sampling effort that might mask the actual variability of the metric in relation to waterbody characteristics and therefore lead to biased assessments of the ecological status (Elliott et al. 2006). Many of the WFD tools developed to assess estuarine fish species richness do not take SAR or SLR into account.

The examination of local species richness by complete census is usually not feasible (Colwell & Coddington 1994), and therefore its assessment relies on sample data. There is often a marked variability in the sampling effort applied to estuaries. In the UK, for example, estuaries like the Thames and the Severn have been intensively sampled for over 40 yr (e.g. Wheeler 1979, Potter et al. 2001, Attrill & Power 2002, Colclough et al. 2002, Henderson & Bird 2010, McGoran et al. 2017), using a variety of sampling methods and resulting in more than 100 fish species being recorded in each estuary (Elliott et al. 2002, Henderson & Bird 2010). In turn, fish assemblage investigation in other UK estuaries (e.g. the Esk(E) and Lune) have only started within the last decade (Environment Agency 2017a), as prompted by the monitoring requirements of the WFD. A higher sampling effort may also be required in larger estuaries to better represent the number of species using the different habitats within the estuary. As a result, the sampling effort (as the number of samples taken) may range over more than an order of magnitude across waterbodies and over the years (e.g. Franco et al. 2008a). This may make it difficult to disentangle the patterns of variability in the observed species richness across estuaries (e.g. SAR and SLR) from differences in sampling effort, thus creating limitations to data comparability and inclusion in the analysis (e.g. Pasquaud et al. 2015). It is generally assumed that with increased sampling, an increasing proportion of the total number of species likely to occur in an estuary will be taken. Therefore, it is expected that the cumulative number of species recorded in the samples increases with increasing sampling effort, generating the so-called species-accumulation curve (Sanders 1968). The curve of species recorded across all samples eventually reaches an asymptote which denotes the total species complement that likely characterises an area. This assumes that even in open systems (such as estuaries) there is a finite number of species which can access the area because of their geographical and habitat/environmental preferences (although of course, global environmental factors such as climate change may cause new species to enter the species pool). Therefore, we hypothesised that a species-accumulation curve can be used to estimate the species complement of estuaries.

A range of sampling methods are used for estuarine fish-based assessment, each method with its own selectivity (Franco et al. 2012, Pérez-Dominguez et al. 2012). A trade-off between data standardisation (hence comparability) and representation of the full species complement of an estuary exists. On one hand, a multi-method approach, as applied for example in WFD fish-based assessment in the UK (Coates et al. 2007) is most likely to provide a more comprehensive picture of the full species complement of an estuary, although the uneven effort distribution and habitat representation of different sampling methods within an estuary may influence the comparability between estuaries. On the other hand, a single sampling method is more likely to produce a standardised approach that allows comparability between estuaries. However, the ability of the estimated species richness to represent the full species complement of any estuary may be limited to a specific part of the assemblage or type of habitat that is more efficiently sampled with the selective gear. This may introduce significant bias when comparing and contrasting species richness in geographically disparate communities sampled with different methods. In turn, this bias is likely reduced in comparative studies and assessments based on the same sampling method, although it must be acknowledged that in these cases, the gear-specific species complement for an estuary can only be estimated. While the use of species-accumulation curves is key to providing standardised estimates of species richness (i.e. the species complement) for an area, independent of sampling effort, studies testing underlying paradigms of biodiversity such as SAR and SLR in estuarine fish assemblages so far have only relied on observed species richness obtained from total lists of species sampled in given estuaries (Pasquaud et al. 2015, Vasconcelos et al. 2015), with the consequent limitations mentioned above. Our study represents the first application of species-accumulation curves (and the derived standardised estimates of the likely gear-specific maximum number of species in estuaries) to the testing of SAR and SLR. In particular, these paradigms were tested at the regional scale by using fish sample data in estuaries located between 51 and 56° N latitude (England and Wales).


Fig. 1. Estuaries across England and Wales that were monitored in the present study

## 2. MATERIALS AND METHODS

### 2.1. Biological data

From May 2006 to November 2013 inclusive, the Environment Agency monitored 27 estuaries across England and Wales for WFD assessment purposes (Fig. 1) using a multigear approach (including fyke nets, seine nets, beam trawls and otter trawls). In 2014 and 2015, Natural Resources Wales continued to monitor the Welsh estuaries only with the same techniques while the Environment Agency monitored only English estuaries in 2014 and 2015. Fish species presence records obtained from the standardised use of a beach seine net (45 m by 3.5 m, with a 5 mm knotless mesh in the centre and 20 mm mesh in the wings) were selected for this study, as this method was the only one providing the widest coverage between and within estuaries across the studied region. The estuaries were selected as a representative group of the variety of estuaries found in England and Wales (UKTAG 2006), with seine netting being undertaken in sites distributed in the lower intertidal and shallow subtidal habitats across the full salinity gradient in each estuary.

The selected dataset included a total of 3578 samples collected at 144 sites, with the number of sites per estuary generally depending on waterbody size (Table 1). Small estuaries (<1000 ha) contained at least 3 to 5 sites, medium-sized estuaries (1000–10 000 ha) contained 5 to 10 sites, and large estuaries (>10 000 ha) contained 10 to 12 sites. Safety and logistical constraints also influenced site selection in some cases (e.g. in the Severn, a large estuary, only 5 sites could be safely sampled with a seine net).

At each site, at least 4 samples were taken annually: 2 in spring (May to June) and 2 in autumn (September to November) given that there are seasonal migrants to estuaries (Potter et al. 2015). The number of samples taken over the period 2006–2015 in each estuary varied from 41 (Medway) to 285 (Thames) (Table 1). Explanatory variables for the SAR and SLR hypotheses were also measured for each estuary (Table 1). Specifically, we recorded waterbody size (measured in ha) and latitude and longitude at the estuary mouth (measured in degrees and decimal minutes) using ArcMap v.9.3.1, with longitude of the estuary

Table 1. Total species caught (observed species richness, $SR_{obs}$), number of sites ($n_{sites}$) and number of samples collected per estuary (n) during surveys from 2006 to 2015 in selected estuaries in England and Wales. Table also shows waterbody size, latitude and longitude, as well as mean site salinity and mean river flows measured over the study period

| Estuary | $SR_{obs}$ | $n_{sites}$ | n | Size (ha) | Latitude | Longitude | Mean site salinity (psu) | Mean fluvial flow ($m^3 s^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Adur | 31 | 5 | 114 | 137 | 50.85 | −0.28 | 15.40 | 0.35 |
| Alde & Ore | 25 | 4 | 52 | 1088 | 52.12 | 1.54 | 29.25 | 0.89 |
| Camel | 45 | 7 | 156 | 1091 | 50.55 | −4.91 | 25.71 | 0.74 |
| Carrick Roads Inner | 55 | 7 | 147 | 1259 | 50.21 | −5.04 | 28.86 | 1.25 |
| Conwy | 37 | 3 | 111 | 1557 | 53.29 | −3.84 | 23.33 | 22.82 |
| Dart | 55 | 5 | 125 | 831 | 50.38 | −3.60 | 20.40 | 13.41 |
| Dee | 52 | 9 | 215 | 10928 | 53.32 | −3.19 | 14.89 | 43.26 |
| Esk(E) | 22 | 4 | 97 | 28 | 54.48 | −0.61 | 20.50 | 5.79 |
| Exe | 42 | 5 | 89 | 1793 | 50.63 | −3.44 | 23.40 | 26.55 |
| Foryd Bay | 36 | 3 | 100 | 243 | 53.11 | −4.32 | 32.33 | 6.17 |
| Humber | 48 | 12 | 237 | 32647 | 53.71 | −0.48 | 8.42 | 139.28 |
| Lune | 25 | 2 | 76 | 302 | 54.02 | −2.83 | 15.00 | 73.20 |
| Medway | 23 | 3 | 41 | 5657 | 51.41 | 0.64 | 21.33 | 12.59 |
| Milford Haven Inner | 34 | 7 | 256 | 2102 | 51.72 | −4.91 | 24.00 | 15.18 |
| Nyfer | 25 | 3 | 107 | 103 | 52.02 | −4.84 | 29.00 | 35.92 |
| Orwell | 38 | 4 | 139 | 1249 | 52.00 | 1.23 | 31.25 | 1.49 |
| Poole Harbour | 49 | 11 | 180 | 3309 | 50.70 | −2.00 | 24.18 | 4.64 |
| Ribble | 34 | 4 | 84 | 4528 | 53.71 | −2.97 | 13.75 | 39.80 |
| Severn | 27 | 5 | 48 | 53645 | 51.81 | −2.54 | 13.60 | 127.03 |
| Southampton Water | 41 | 8 | 236 | 3091 | 50.87 | −1.36 | 26.88 | 21.69 |
| Stour | 36 | 5 | 127 | 2553 | 51.95 | 1.18 | 30.20 | 0.97 |
| Taw/Torridge | 32 | 8 | 171 | 1461 | 51.07 | −4.16 | 21.63 | 37.28 |
| Tees | 27 | 2 | 74 | 1143 | 54.62 | −1.18 | 26.00 | 27.20 |
| Teifi | 26 | 3 | 75 | 616 | 52.11 | −4.69 | 13.33 | 35.92 |
| Thames | 34 | 8 | 285 | 24842 | 51.49 | 0.25 | 7.63 | 82.59 |
| Tweed | 25 | 5 | 123 | 244 | 55.76 | −2.04 | 9.20 | 13.90 |
| Wyre | 29 | 2 | 44 | 637 | 53.88 | −2.98 | 18.00 | 8.71 |
| Min | 22 | 2 | 41 | 28 | 50.21 | −5.04 | 7.63 | 0.35 |
| Mean | 35.3 | 5 | 130.0 | 5818 | 52.29 | −2.27 | 21.02 | 29.58 |
| Max | 55 | 12 | 285 | 53645 | 55.76 | 1.54 | 32.33 | 139.28 |
| SD | 10.1 | 3 | 67.7 | 12195 | 1.50 | 2.11 | 7.29 | 36.63 |

also being recorded as a possible covariate. Additional variables characterised the estuarine conditions: mean site salinity (measured as practical salinity units) was calculated using salinity data collected by the Environment Agency between 2006 and 2015 (G. Phillips unpubl. data); mean freshwater flow rates (measured as $m^3 s^{-1}$) over the study period for each estuary were also recorded, using data from the Environment Agency hydrometric monitoring sites stored on the Water Information Management System[1].

### 2.2. Analyses

Using EstimateS (v.9.1.0), rarefaction (interpolation) curves were created for each estuarine dataset following the method for sample-based interpolation provided by Colwell et al. (2012). Species-accumulation curves were created from the cumulative number of species recorded in consecutive samples, with the sample order being randomised within each estuary dataset. A Bernoulli Product Model was used to create the rarefaction curve for each estuary based on the mean value of 999 randomised re-runs, without replacement (i.e. each sample was selected only once). The resulting rarefaction curves provide values of cumulative species richness (SR) in an estuary as a function of the number of samples taken (n), up to the observed total species richness ($SR_{obs}$), as resulting from the totality of samples collected in the estuary. A non-parametric estimator for species presence data, the bias-corrected form of Chao2 (Gotelli & Colwell 2011), was used to extrapolate the mean asymptotic value of the rarefaction curve, representing the maximum species richness ($SR_{max}$) achievable in an estuary (the gear-specific species complement). The 95% confidence interval limits ($CL_{upper}$ and $CL_{lower}$) associated with the mean $SR_{max}$ value were also calculated. In cases where the ratio of the standard deviation to the mean was >0.5, both the bias-corrected and classic forms of the Chao2 method

[1]https://data.gov.uk/dataset/0bac3947-c632-47eb-83d5-fff7f1911537/hydrometric-monitoring-points

were used, and the largest of the 2 resulting mean $SR_{max}$ values was selected as the best estimate (Colwell 2013). To discern any potential groupings of the estuaries according to their estimated (gear-specific) fish species complement, a cluster analysis (with SIMPROF) was undertaken between estuaries based on the mean $SR_{max}$ and the associated confidence limits. The analysis was undertaken in Primer v6.1.2 using Euclidean distance, group average cluster algorithm and 5% significance level for the SIMPROF test.

The SAR and SLR paradigm hypotheses were tested using generalised additive models (GAMs). Estuary size and latitude were used as explanatory variables for $SR_{max}$, and longitude was also included as a possible covariate. The small size of the dataset (27 estuaries) prevented the inclusion of all 3 variables in a single model, and therefore a modelling strategy was adopted whereby 3 models (M1–M3) were generated including all possible combinations of pairs of the 3 variables (M1 with size and latitude as predictors, M2 with latitude and longitude, M3 with size and longitude) to account for possible combined effects. GAM was undertaken using the 'mgcv' package in R (Wood 2006, R Core Team 2017) with the following parameters specified: negative binomial family (with log link function); thin plate regression splines as smoothing functions for all explanatory variables (with default basis dimension $k$ = 10, except for latitude in M2, where $k$ was set to 18, the maximum value for $k$ allowed by the dataset size); an additional penalty added on the null space of the original penalty for all covariates (select = TRUE); and REML used as smoothness selection method. Model diagnostic was undertaken (checking of residuals for assumptions, overfitting and overdispersion) to assess the validity of the models. The significance of the model predictors was assessed based on model summary results, and the deviance component explained by each individual predictor in the model was assessed as an indicator of the magnitude of the effect, by comparing nested models (i.e. M1, M2 and M3 against models calibrated for individual variables using the same model parameters (as described above) using hypothesis testing ('anova.gam' function in R).

## 3. RESULTS

### 3.1. Fish assemblage composition

Across all estuaries in the study, 114 species were recorded (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m613p125_supp.xlsx). The total $SR_{obs}$ ranged from 22 (Esk(E)) to 55 (Carrick Roads Inner and Dart) with a mean ± SD of 35.3 ± 10.1 (Table 1). Five of the 114 species were encountered in every estuary (European flounder *Platichthys flesus*, European plaice *Pleuronectes platessa*, common goby *Pomatoschistus microps*, sand goby *Pomatoschistus minutus*, European sprat *Sprattus sprattus*), and 20 species were recorded in only 1 estuary (Table S1). The taxa were listed per estuary, and following Franco et al. (2008b), they were categorised into 1 of 6 estuarine use functional guilds, based upon the way that the species use an estuary (Table S1). Of the 114 species recorded in this study, 32 were classified into more than 1 category by Franco et al. (2008b). Two are considered catadromous (European eel *Anguilla anguilla* and thin lipped grey mullet *Liza ramada*), with the thin lipped grey mullet also considered a marine migrant in some estuaries. Seven are anadromous, with the three-spined stickleback *Gasterosteus aculeatus* and sea trout *Salmo trutta* being the most frequently encountered in estuaries across the study area. Twenty are categorised as estuarine species (common goby and sand goby caught most frequently in this group; 27 estuaries). Of the 24 freshwater species encountered in the study, the most common included roach *Rutilus rutilus*, Eurasian minnow *Phoxinus phoxinus* and common dace *Leuciscus leuciscus*.

Of the 15 marine migrants encountered in the study, European flounder, European plaice and European sprat were caught in all estuaries in the study, although flounder is also regarded as semi-catadromous given that it spends most of its time in estuaries after breeding at sea (Potter et al. 2015). The most numerous category of fishes in the study was marine stragglers, with 31 species caught in the study area. The longspined sea scorpion *Taurulus bubalis* and great sandeel *Hyperoplus lanceolatus* were the most frequent, caught in 16 and 15 estuaries, respectively.

Forty species were consistently present in at least 90% of the samples taken per estuary (Table S1), thus characterising the dominant assemblage for each estuary for the geographical area covered by this study. Per estuary, either 11 or 12 species were caught in ≥90% of samples, apart from the Severn, with 16 species listed. The common goby, sand goby and European sprat were consistently caught in 26 of the 27 estuaries, with European flounder being the only species that was caught in ≥90% of the samples in every estuary.

Two species of the wrasse family, corkwing wrasse *Crenilabrus melops* and ballan wrasse *Labrus ber-*

*gylta*, were caught consistently in the southwest of the study area (Carrick Roads Inner and Dart, respectively). Three species of sandeels were consistently recorded (small sandeel *Ammodytes tobianus*, Corbin's sandeel *Hyperoplus immaculatus* and great sandeel) and 3 clupeids were also present (herring *Clupea harengus*, European pilchard *Sardina pilchardus* and European sprat), as were 4 cyprinids (common bream *Abramis brama*, common dace, Eurasian minnow and roach). Three gadoids were caught consistently (Atlantic cod *Gadus morhua*, whiting *Merlangius merlangus* and pollack *Pollachius pollachius*) and 5 gobies (black goby *Gobius niger*, two spotted goby *Gobiusculus flavescens*, common goby, sand goby and painted goby *Pomatoschistus pictus*).

### 3.2. Species-accumulation curves

The species rarefaction curves are similar in overall shape for each estuary, with the first 50 samples providing the steepest part of the species accumulation (Fig. 2). Three of the 27 estuaries had 50 or more species recorded (Carrick Roads Inner, Dart and Dee), 2 of which reached over 50 species within 100 samples (Carrick Roads Inner, Dart).

Some estuaries, such as the Taw/Torridge and the Thames, had a pronounced profile of a steep gradient in the first 50 samples with the curve quickly levelling off thereafter. The Thames was the most highly sampled estuary in the dataset, with a total of 285 samples, yet few species were caught ($SR_{obs}$ = 34). For the Thames, when n = 50, SR = 24, i.e. 71% of total observed number of species was detected within 18% of the samples collected, with the remaining 10 species being recorded over the next 235 samples. The profiles of other estuaries such as the Severn and Southampton Water had a less pronounced levelling off phase. With Southampton Water, when n = 50, SR = 26 (63% of total observed species richness with 21% of samples), with the remaining species being recorded over the further 186 samples. This suggests that not only does Southampton Water harbour more species (41 compared to 34 for the Thames), but also that the recorded species are more evenly spread throughout all of the samples, thus requiring more effort to gain an understanding of the entire species composition that can be sampled with the seine net. The steep profile of the Severn is exacerbated by the low number of seine net samples (n = 48) collected in this estuary over the studied period.

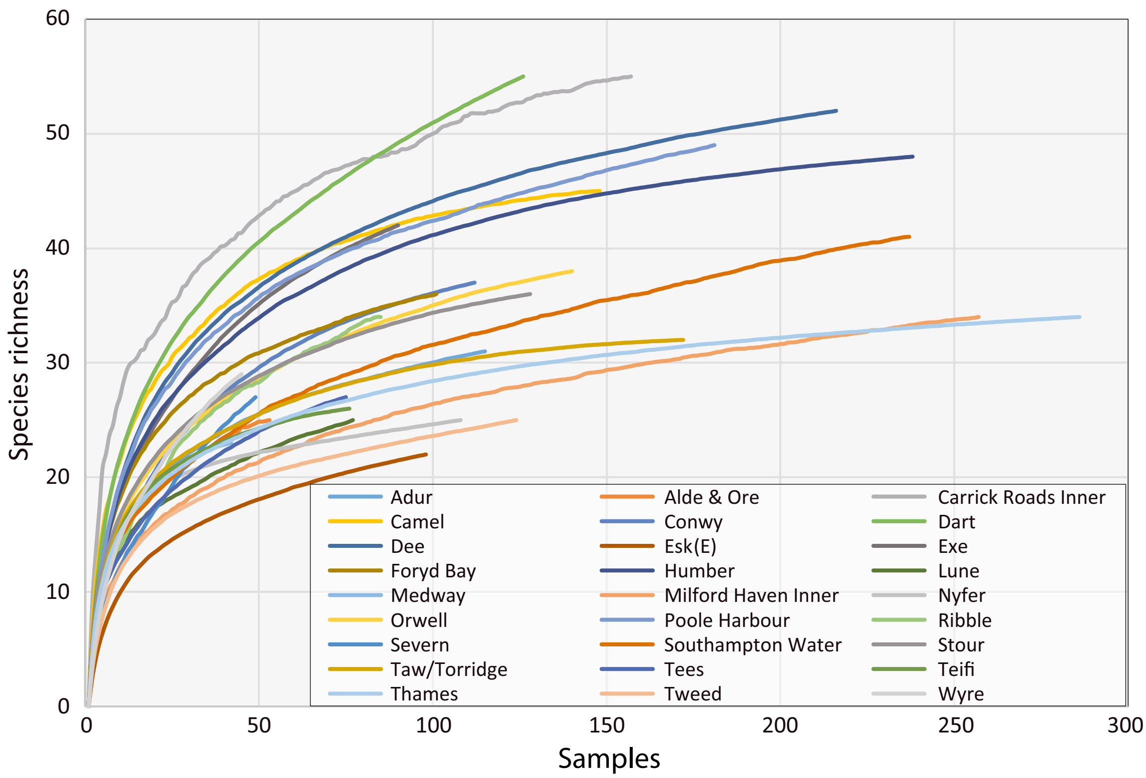


Fig. 2. Rarefaction curve for pooled data per estuary. Each curve represents the mean of up to 999 randomisations

### 3.3. Estimated $SR_{max}$

$SR_{max}$ calculated for the studied estuarine fish assemblages (as sampled by seine net) ranged from 24.39 (Medway) to 73.97 (Dart), with an overall mean ± SD of 42.08 ± 12.54 species (Table 2). The total percentage of sampled species compared to the estimate of asymptotic species richness ($SR_{obs}/SR_{max}$) that could be caught by seine netting in the studied estuaries ranged from 55% (Tweed) to 100% (Taw/Torridge).

### 3.4. SAR and SER hypothesis testing

The 3 models calibrated to test the SAR and SLR hypotheses respectively explained 68.7% (M1, size and latitude as predictors), 57.5% (M2, latitude and longitude) and 19.5% (M3, size and longitude) of the total deviance in $SR_{max}$ data. Latitude was always a highly significant predictor in the 2 models in which this variable was included (M1 and M2). Both models indicated a net decrease in species richness with increasing latitude, with this decrease being particularly marked between 50 and 52° N (Fig. 3). Some fluctuations (secondary maxima) were observed at latitudes around 53 and 56° N due to the higher species richness recorded in the Dee, Humber and Tweed compared to other estuaries at similar latitudes (Table 2). Estuary size was also a significant predictor, albeit only when coupled with the latitudinal effect in M1, with the species richness increasing with increasing estuary size (Fig. 3). The latitudinal effect was in general larger than the size effect, as indicated by the deviance explained by each of these predictors in the models (Fig. 3).

Table 2. Estimated maximum species richness ($SR_{max}$) with 95% confidence limits (CL) for all sampled estuaries. Groupings as identified by cluster analysis (see Fig. 4) are also reported

| Estuary | $SR_{max}$ | $CL_{lower}$ | $CL_{upper}$ | Group |
|---|---|---|---|---|
| Medway | 23.37 | 23.03 | 28 | A1 |
| Esk (E) | 25.71 | 22.63 | 43.82 | A1 |
| Teifi | 26.49 | 26.04 | 32.15 | A1 |
| Lune | 30.18 | 25.98 | 52.28 | A1 |
| Tees | 30.45 | 27.64 | 45.67 | A1 |
| Taw/Torridge | 32.14 | 32.01 | 35.23 | A1 |
| Wyre | 33.4 | 30.01 | 48.24 | A1 |
| Thames | 37.32 | 34.5 | 56 | A2 |
| Stour | 37.86 | 36.29 | 47.91 | A2 |
| Foryd Bay | 39.47 | 36.64 | 54.73 | A2 |
| Orwell | 41.47 | 38.69 | 55.46 | A2 |
| Conwy | 41.62 | 37.94 | 59.65 | A2 |
| Camel | 45.85 | 45.09 | 52.93 | A2 |
| Alde & Ore | 32.36 | 26.3 | 66.77 | A3 |
| Nyfer | 34.91 | 26.86 | 77.68 | A3 |
| Severn | 37.77 | 29.82 | 68.14 | A3 |
| Adur | 37.94 | 32.33 | 67.25 | A3 |
| Milford Haven Inner | 41.17 | 35.59 | 66.26 | A3 |
| Ribble | 45.12 | 36.62 | 81.19 | A3 |
| Exe | 48.8 | 43.69 | 69.38 | A4 |
| Humber | 50.49 | 48.41 | 63.22 | A4 |
| Carrick Roads Inner | 58.97 | 55.85 | 73.52 | A4 |
| Tweed | 45.83 | 30.04 | 111.08 | B |
| Southampton Water | 60.42 | 46.19 | 113.62 | B |
| Dee | 60.96 | 54.12 | 89.86 | B |
| Poole Harbour | 62.13 | 52.42 | 99.34 | B |
| Dart | 73.97 | 61.1 | 113.97 | B |

### 3.5. Estuary groupings

According to the classification analysis (cluster and SIMPROF) based on $SR_{max}$ data (mean and confidence limits), a group of 5 estuaries (Tweed, Dee, Poole Har-

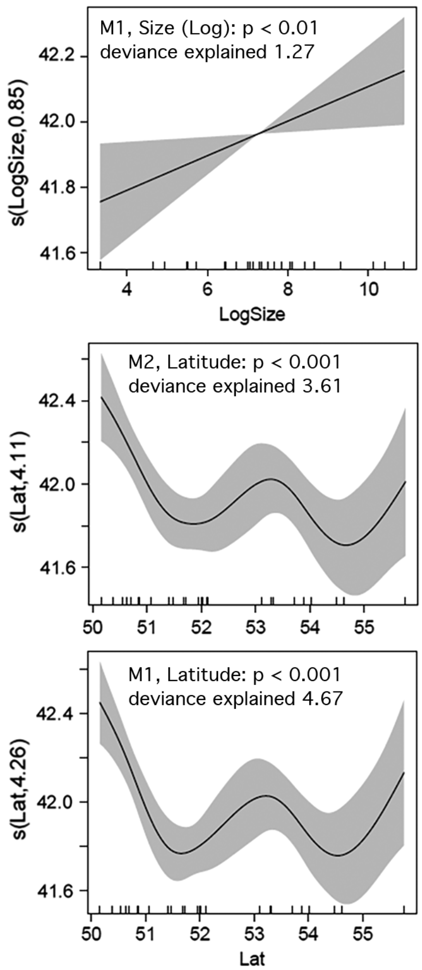


Fig. 3. Generalised additive modelling smoothing curves for significant predictors of maximum species richness, with associated confidence interval (shaded area). Significance and magnitude of the effect (deviance explained by the individual predictor in the model, [M]) are indicated. Curves have been rescaled to reflect variability on the $SR_{max}$ scale

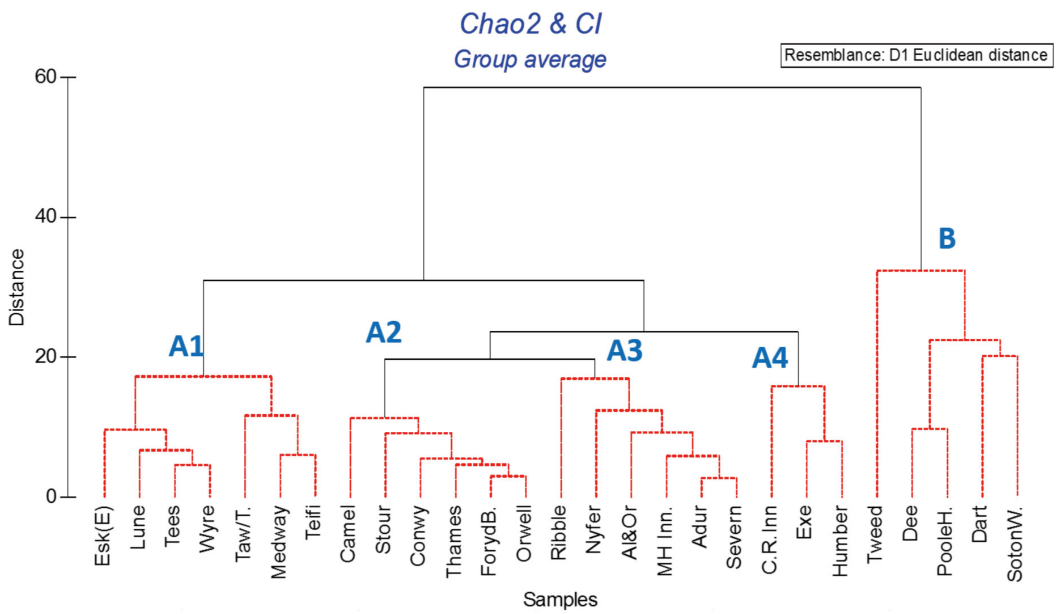


Fig. 4. Cluster analysis of the studied estuaries based on maximum species richness estimates (mean and confidence limits). Significantly different groups (SIMPROF, $p < 0.05$) are indicated with solid black lines. Groupings are indicated (A1–A4, B)

bour, Dart and Southampton Waters; Table 2, Fig. 4) significantly ($p < 0.05$) differentiated from the others due to the generally higher mean $SR_{max}$ values (ranging from 46 to 74; in most cases >60, overall group mean of 61), although the highest uncertainty was associated with these mean estimates (confidence limit interval between 37 and 81; 57 on average). The estuaries in this group are of variable size (ranging from 244 to 10 928 ha; average = 3681 ha) and are located between 50.4 and 55.7° N (52.2° N on average).

The remaining 22 estuaries had variable mean $SR_{max}$ values, between 23 and 59 (mostly <50), and they further differentiated ($p < 0.05$) into 4 groups (A1–A4; Table 2, Fig. 4). Group A1 comprises 7 estuaries (Medway, Esk, Telfi, Lune, Tees and Taw/Torridge) of small/medium size (28 to 5657 ha; average = 1406 ha) and located between 51.1 and 54.6° N (53.1° N on average). These estuaries had the lowest mean $SR_{max}$ (always <34; group average = 29) compared to the other estuaries, with the highest confidence associated with these estimates (confidence limit interval of 14 species on average, generally <26). Groups A2 and A3 each comprised 6 estuaries (Table 2) and had intermediate values of mean $SR_{max}$ (mostly around 40, ranging from 32 to 46 overall). However, the uncertainty around these mean estimates differed between the 2 groups, being higher in A2 (confidence limit interval of 16 species on average) and lower in A3 (confidence limit interval of 40 species on average). Estuaries from these 2 groups are located at latitudes between 50.5 and 53.7° N (with an average value close to 52° N in both groups), and most of these estuaries are of medium size (around 1500 ha), with the notable presence of 1 large estuary in each group (Thames in A2 and Severn in A3). Group A4 only comprised 3 estuaries (Exe, Humber and Carrick Roads Inner) that are of medium to large size (1259–34 647 ha, average = 11 900 ha) and are located at a lower latitude than the others, on average 51.5° N, ranging from 50.2 to 53.7° N). These estuaries had higher mean $SR_{max}$ values (between 49 and 59; average = 53), with a relatively low uncertainty (confidence limit interval of 19 species on average).

## 4. DISCUSSION

### 4.1. Fish species complement of estuaries, SAR and SLR paradigms and other possible influencing factors

Examining the relationships of localised assemblages from varied study areas and effort using rarefaction curves has proven successful in tree and insect studies (Colwell et al. 2012), although this approach has rarely been used for fishes. Quantifying biodiversity using rarefaction curves and asymptotic estimators is a method not often used for estuarine fish assemblages at a regional scale. Most of the studies investigating fish species richness in estuaries and their patterns in relation to natural and/or anthropogenic variability are based on surveys that are assumed to be a complete census of a localised assemblage, without necessarily considering the implications of varying sample effort and/or methods on the completeness of the assemblage that has been measured (Franco et al. 2008b, Nicolas et al. 2010a,b, Vasconcelos et al. 2015).

In the present study, before any hypotheses were examined, an objective examination of the effectiveness of the sampling to obtain a species census was firstly undertaken by estimating the maximum number of species in each estuary that can be caught using a seine net. The estimator used in this study for the sample-based incidence data is well proven in a variety of ecological fields (Chao 1987, Shen et al. 2003, Gotelli & Colwell 2011, Chao et al. 2015). We acknowledge that the approach we used in this paper is not free from limitations. The purpose of applying rarefaction curves in our study was to obtain standardised species richness data to allow comparing and contrasting between estuaries and as such the ability to examine and explore the SAR and SLR paradigms set out in this paper. Therefore, we chose to select fish data from a single sampling method (seine netting) that has been used in a consistent and standardised way across the studied estuaries, to allow better control of the effects of sampling variability and effort. As a result, the approach applied in this paper cannot be considered to be a complete census of the fish assemblage present in an estuary, due to the limitations imposed by the selectivity, efficiency and habitat sampled with the selected method. The calculation of estimated total species richness is bounded by this method and must be considered as a gear-specific indicator of the fish species complement of an estuary. Although in absolute terms, the resulting estimates may differ compared to the known species richness from other studies using multiple or different sampling methods (as discussed in detail further below), we are more confident that the standardised estimates we used allow us to do a more robust comparison between estuaries, while controlling for the effects of sampling variability and effort.

The latitudinal gradient in diversity has been examined for over 2 centuries, and the attenuation of species diversity as one travels further from the equator has been recorded by multiple authors examining many biota and regions (Jablonski et al. 2017). However, the causal processes that drive this phenomenon remain elusive (Hillebrand 2004). Several hypotheses have been proposed to explain this phenomenon, which Brown (2014) grouped into 3 main categories: phylogenetic niche conservatism, ecological productivity and kinetics.

Wiens & Donoghue (2004) considered that species' ancestral niches were tropical, preventing widescale adaptation to temperate niches in recent history due to factors such as glaciation. In the case of the study area, this phylogenetic niche conservatism hypothesis is not considered to be a causal process for the latitudinal pattern observed in this study. The northern estuaries were covered by an ice sheet for longer, although the interconnected nature of the UK waters would suggest that this is no longer a factor 11 000 yr after the last glaciation.

An ecotone, representing a change in ecological productivity, is the boundary between biogeographic regimes where there is merging of 2 adjacent assemblages, and so the ecotone has elements of both assemblages and thus can be richer than either of the merged elements (Basset et al. 2013). In the case of the British Isles, the influence of the North Atlantic Drift especially on southwestern areas exacerbates the mixing of Boreal and Lusitanian faunae (Henderson & Henderson 2017). Therefore it would be valuable in the future to categorise the estuarine fish assemblage members according to their Boreal and Lusitanian origins to show where the warmer Lusitanian fauna from the Iberian Peninsula merges with the colder Boreal community from NW Europe and the North Sea (Wheeler 1969). Furthermore, there is a depth effect between the shallow North Sea to the east compared to the deep waters off the coastal shelf to the west, suggesting that a longitudinal element would have some effect on patterns of diversity in this regional study, as has been previously reported (Nicolas et al. 2010b). However, the inclusion of longitude in the models in the present study does not support relationships between longitude and species diversity, or a combination of longitude with latitude and species diversity (see below).

By detailing the observed latitudinal gradient in many biological realms, Fischer (1960) reviewed studies detailing the observed latitudinal gradient in many biological realms and concluded that this phenomenon is illustrated best in the marine field and that climates with higher and consistent temperatures support higher diversity. Brown (2014) noted that greater rates of metabolism, ecological dynamics and coevolutionary processes are all supported by higher temperatures. In the context of estuarine fish ecology, higher temperatures at lower latitudes, leading to higher biological rates, have also been suggested as leading to biogeographic differences (Henriques et al. 2017), perhaps due to shorter generation times and higher mutation rates (Gaston 2007). This kinetic argument is considered to be the most likely cause of the latitudinal gradient shown here. Multiple agencies across the marine field now record extensive thermal measurements in inshore waters. The diversity–temperature relationship could be further explored by integrating existing temperature records with this biological dataset. In supporting the SER of species richness and latitude, this study suggests that increases in sea temperatures as a result of climate change could increase diversity in estuarine fish species richness in temperate waters (Attrill & Power 2002, Henderson 2007, Hiddink & Ter Hofstede 2008, Robins et al. 2016). This may also result in increased abundance, although density-dependence has been shown to be a limiting factor on the abundance of sprat in the Bristol Channel (Henderson & Henderson 2017).

The SAR also proved significant, although the effect was only noticeable when combined with latitude. This is in contrast to previous studies which have found the relationship between size and estuarine fish diversity to be highly significant (Harrison & Whitfield 2006, Franco et al. 2008a, Nicolas et al. 2010a). It is assumed that a larger sample area would contain more individuals as well as more species (Whittaker & Fernández-Palacios 2007), perhaps due to habitat heterogeneity opportunities over a larger area (Báldi 2008).

At the global extent, Vasconcelos et al. (2015) found that species richness of marine fish correlated highly with latitude, with estuary size being only important at the regional extent. Our study indicates that estuary size alone is not sufficient as a driving influence on species richness. Of the 3 estuaries with surface areas greater than 20 000 ha (Humber, Thames and Severn), the Humber is the only estuary that recorded high diversity with either observed species or predicted total richness. The high diversity measured in the Humber cannot be explained by high heterogeneity, as the Humber contains as many large-scale habitats as the Thames and many fewer than the Severn (JNCC 2015).

Unlike the Humber, the Thames had few observed species of both marine guilds and estuarine species, and therefore the overall species richness was comparatively poorer. The Thames, despite its southerly latitude, has a relatively narrow shelf providing few marine species to the assemblage, and even then the uniform sedimentary habitats of the southern North Sea create fewer niches and thus species (Ducrotoy et al. 2000). By classifying the habitat attractiveness for fishes in an estuary, Amorim et al. (2017) noted potential changes to the functioning of the fish community and the nursery carrying capacity over time. A similar approach could be used spatially with this dataset to further investigate the relationships between habitat types and fish communities in the Thames and the rest of the estuaries in the study area. The Thames only started to regain its estuarine fish community in the 1960s after many decades of being abiotic (Elliott et al. 2006, Taylor 2015, Henderson 2017). Furthermore, the Thames has been subject to severe and sustained environmental degradation (Coates et al. 2007), notably habitat loss, particularly in the mid and upper reaches of the estuary and the presence of a water quality barrier due to low dissolved oxygen, and these factors may have contributed to reduce the species richness in this estuary. Significant pollution events continue in the Thames catchment (Environment Agency 2017b). By further exploring the relationship between species richness drivers such as habitat functioning as well as anthropogenic factors such as pollution events, it may be possible to further explain the pattern of differentiation between not only the Thames assemblage but also the estuarine populations described in this paper.

The historical sampling of the Severn Estuary fish assemblage gives the opportunity to validate the analysis in this paper. This estuary is considered to be one of the most diverse estuaries in the UK (Potts & Swaby 1993) and was designated under the Ramsar Convention in 1995 (JNCC 2008). Only 27 species were recorded in the Severn in this study, and this shows the influence of both differing sampling methods and a greater sampling effort in previous studies. Using once-monthly power station sampling at the edge of a large intertidal mud flat, in the greater Severn estuary, Henderson & Bird (2010) recorded a total of 83 species over 28 yr, with a notable predominance of species of marine origin in the assemblage (77 % of the species), compared to the present study (59 %). While $SR_{max}$ is estimated to be much higher than $SR_{obs}$ for the Severn estuary, the $SR_{max}$ value predicted in this study (38) is still far lower than the 83 species recorded by Henderson & Bird (2010). This is probably the result of the intense nature of power station sampling compared to seine netting. Therefore, while further seine net sampling is expected to reveal more species, the nature of the method is not expected to yield similar numbers of taxa as reported by Henderson & Bird (2010) or Potts & Swaby (1993).

Despite the Tweed being the most northerly and one of the smallest estuaries in the study, it had one of the highest estimated $SR_{max}$ values (46). However, a high uncertainty is associated with this estimate, as attested by the large confidence interval (the largest of all assessed estuaries), suggesting that caution needs to be applied when drawing conclusions regarding its estimated maximum value. Continued sampling may help to increase confidence in the overall assessment. In terms of species presence in estuaries, only a few species are adapted to the life in changing environments such as estuaries (and these are highly abundant, confirming the stress-subsidy continuum; see below). Most of the species occurring in estuaries are transient species, either migratory species or stragglers (Franco et al. 2008a), with most of the contribution to species diversity coming from the marine realm rather than from fresh waters (Whitfield et al. 2012). The dominance of marine taxa as a proportion of the overall fish species richness of an estuary is well defined (Potter et al. 1990, 2015, Pease 1999, Whitfield 1999) and is consistent throughout the study area and the current estuarine datasets present, with some notable exceptions. Categorising the marine species into those that generally inhabit coastal areas and only enter estuaries accidentally and in low numbers (marine stragglers) and those that often spawn at sea and enter estuaries in high numbers, particularly as juveniles in defined patterns (marine migrants), aids understanding of both natural and anthropogenic impacts on estuaries (Elliott et al. 2007b).

In accordance with the literature, a higher proportion of marine straggler species appears to characterise the estuaries where a higher overall species diversity was estimated in this study (e.g. Tweed, Dee, Poole Harbour, Dart and Southampton Waters). The width of the estuary mouth was an important predictor of species richness, particularly marine species, in previous studies (Pease 1999, Roy et al. 2001, Nicolas et al. 2010b, Tweedley et al. 2017). However, the high diversity estuaries mentioned above do not show particularly large mouths compared to other estuaries with less diverse fish assemblages (as, for example, the Severn). We argue that it is the mouth width to estuary size (e.g. area) ratio rather than the mouth width in itself that affects the predominance of marine species occurring in the estuary as a whole, as this not only accounts for the accessibility of the estuary to species entering from the adjacent marine area, but also the penetration of these species into the estuary and their distribution across estuarine habitats (likely to be enhanced where the mouth to estuary size ratio is higher, resulting in the estuary resembling more a marine embayment). This argument appears to be supported by the findings by Pérez-Ruzafa et al. (2007) on the hydrographic and geomorphologic determinants of fish assemblages in coastal lagoons. These authors found that a morphometric parameter (named restriction ratio) measuring the ratio between the width of the lagoon entrances and the lagoon perimeter (a proxy for the waterbody size) was amongst the primary constraints affecting the fish assemblage composition in the lagoons, mainly through influences on the temperature and salinity regime of these systems. The latter factor is of particular relevance to the entrance and penetration of estuaries by stenohaline marine species such as marine stragglers.

The presence of some straggler species permeating throughout certain estuaries and their presence in nearly all samples collected across those estuaries challenges the expected biological preferences of those species, or their functional categorisation for the estuaries within this study. Exploring those estuaries that are of particular significance to the unexpected 'generalists' with extended sampling may explain how these species adapt and thrive across the highly heterogeneous and challenging estuarine environment.

The above feature reflects the so-called stress–subsidy continuum, whereby variable conditions in estuaries are stressful for those species not adapted to them but a subsidy for those that are adapted (Elliott & Quintino 2007). For example, some species are ubiquitous and euryecious, such as the European flounder (Borg et al. 2014, Vinagre et al. 2005), and its presence in all areas of the 27 estuaries in this study underlines its importance to estuarine fish assemblages. It has been noted, however, that there can be changes even to this species due to both natural and anthropogenic factors (Amorim et al. 2017), with a major decrease in European flounder recorded in a Portuguese estuary (Cabral & Costa 1999), possibly due to climate change (Cabral et al. 2001).

A notable exception to the patterns mentioned above is the high fish diversity observed and estimated in this study for the Humber, which resulted from a particularly high number of freshwater taxa. The high percentage of freshwater taxa in the Humber may be due to the large catchment and high fluvial flow, resulting in low overall site salinity despite the sites being located in the oligohaline, mesohaline and polyhaline areas, allowing freshwater taxa to actively or passively occur in greater numbers into the estuary.

The influence of a latitudinal–longitudinal combination factor (i.e. SW to NE) rather than either on its own is expected to be important in the context of the British Isles, given that the SW has the larger influence of the warmer waters of the North Atlantic Drift and the NE the influence of colder North Sea waters (Nicolas et al. 2010b). If the estuarine fauna was therefore mainly the result of the influence of its shelf components (the marine migrants and the straggler species), then this would have a dominating effect, as has been found previously (Vasconcelos et al. 2015). Accordingly, the main influence would be a gradient from the SW to the NE of the study area, but longitude was not a significant explanatory variable of species richness in our study.

### 4.2. Implications for monitoring and management

The size and nature of the full fish species complement of an estuary are regarded as indications of the ecological status and so management measures are required if that status falls below what is expected. This is the central raison d' être of determining 'Good Ecological Status' under the EU WFD (Hering et al. 2010). The determination of the asymptote and the number of samples required to achieve it is therefore important for managers who have to allocate sufficient resources to quantify and understand the ecological status of an estuary.

Examination of the rarefaction curves suggests that in most estuaries, most of the species richness (that can be sampled with a seine net) is achieved within 100 samples, beyond which continued sampling provides relatively few additional taxa. This analysis not only shows what proportion of the assemblage has been encountered with the available sampling, but it can also be used proactively to define the field methods to help managers understand when continued and further sampling is required. As mentioned before, each method for monitoring fishes in estuaries will sample a slightly different component of the assemblage, and several methods are needed concurrently in order to sample all species (Elliott et al. 2002). The WFD requires using the fish species complement as a predominant factor and metric in determining the health and ecological status of an estuary (Coates et al. 2007). It is therefore emphasised that multi-gear surveys provide an effective way to reach the full species complement. However, due to the heterogeneous and harsh nature of estuarine environments, it is difficult to obtain the entire species complement and so such a survey is not cost effective.

The current study suggests that regional classification tools, such as those aimed at ecological status assessment (Directive 2000/60/EC; WFD 2000), that do not take latitude and estuary size into account may misrepresent the anthropogenic influences on estuaries as species richness decreases with latitude, and, in certain conditions, increases with size, irrespective of anthropogenic impact (acknowledging the variable impacts across the estuaries presented in this study).

Through the driver of the WFD, competent authorities now have extensive information on the hydromorphological attributes of estuaries, including the width of the estuary mouth. Coupled with the ever-increasing biological data, it is recommended that the complex interactions are explored to determine if any factors beyond SLR and SAR influence fish diversity in temperate estuaries.

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